



## Revalidation of the genus *Ectreopopterus* Fowler (Teleostei: Characiformes), with the redescription of its type species, *E. uruguayensis*

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### Abstract

*Ectreopopterus uruguayensis* Fowler 1943 is redescribed based on the holotype and new series of additional specimens from the río Uruguay, río Negro, and small coastal rivers in Uruguay draining to the río de La Plata. Previously proposed synonyms of *Ectreopopterus* Fowler 1943 to *Megalamphodus* Eigenmann 1915 and *Hyphessobrycon* Durbin 1908 are tested and refuted. A new diagnosis is presented for the genus based on the following apomorphies: foramen in posterior region of metapterygoid forms an incomplete arch, bordered posteriorly by the hyomandibula; pectoral-fin rays bearing hooks; posterior margin of second infraorbital posteroventrally oblique and second infraorbital ventrally bordering anterior region of third infraorbital; fourth infraorbital more developed longitudinally than dorsoventrally; ascending process of premaxilla reaching just anterior end of nasal; and lateral line interrupted.

**Key words:** Characidae, *Hyphessobrycon*, *Megalamphodus*, Neotropical fish

### Resumo

*Ectreopopterus uruguayensis* Fowler 1943 é redescrita com base na análise do holótipo e séries novas de espécimes adicionais procedentes das drenagens do rio Uruguai, rio Negro e pequenos rios costeiros afluentes do rio da Prata no Uruguai. Propostas anteriores de sinonímia de *Ectreopopterus* Fowler 1943 com *Megalamphodus* Eigenmann 1915 e *Hyphessobrycon* Durbin 1908 são testadas e refutadas. Uma nova diagnose é proposta para o gênero com base nas seguintes apomorfias: forame na região posterior do metapterigoide forma um arco incompleto, margeado posteriormente pelo hiomandibular; raios na nadadeira peitoral com ganchos; margem posterior do segundo infraorbital oblíqua posteroventralmente, margeando ventralmente a região anterior do terceiro infraorbital; quarto infraorbital mais desenvolvido longitudinalmente do que dorsoventralmente; processo ascendente da pré-maxila alcançando a extremidade anterior do nasal; e linha lateral ininterrompida.

### Introduction

*Megalamphodus* (*Ectreopopterus*) *uruguayensis* Fowler 1943 was described as a new subgenus and species of *Megalamphodus* Eigenmann 1915, based on a single specimen (Fig. 1) collected by Dr. Florentino Felippone in 1935 in Uruguay. Even though the species described by Fowler can be considered valid based on its morphological distinctiveness among characids, the discussion of the status of the generic level name *Ectreopopterus* has been neglected in most of the literature on characid relationships, due to the historical lack of specimens for analysis and to the poor diagnosis presented by Fowler to the subgenus.

Characters that lead Fowler (1943) to describe the new species in *Megalamphodus* were briefly described as the “general scalation [sic], size of the scales, long maxillary, longer lower jaw”, without further discussion. The new subgenus *Ectreopopterus* was diagnosed by “the absence of maxillary teeth, the postorbital in contact with the preopercle, the occipital fontanel a continuous narrow groove, besides both caudal and anal bases the chest and breast also scaled, and the upper caudal lobe shorter than the lower”.

Later, Géry (1972:14) redescribed the holotype (the single specimen so far available), but found some discrepancies in Fowler's description. The holotype, for example, bears a large number of maxillary teeth, whose putative absence was previously used by Fowler (1943) to justify the creation of the new subgenus *Ectreopopterus*. Géry (1972), however, listed four characters that "could be considered, in that critical and over-split group, as subgeneric, but also stated based on the same characters, that "*Ectreopopterus* would then be available for the seven or eight species known that do not seem to be congeneric with *Megalamphodus megalopterus* Eigenmann 1915". No taxonomic action, however, was taken by Géry (1972). Similar to those given by Fowler (1943), the four characters given by Géry (1972) are also related to the fontanels (fontanels narrow *versus* broad), infraorbitals (infraorbital 3 incomplete *versus* complete; infraorbitals 4 and 5 relatively broad instead of being much reduced), and squamation (predorsal line irregularly scaled). The species was later referred as *Megalamphodus uruguayensis* by Géry (1977) without further comments on the status of *Ectreopopterus*.

*Ectreopopterus* was tentatively considered a junior synonym of *Hyphessobrycon* Durbin 1908, along with *Megalamphodus*, by Weitzman and Palmer (1997). Its type species was referred as *Hyphessobrycon uruguayensis* in an annotated list of possible rosy tetras given in the Appendix 1 of that paper. The justification of the new combination was based on the examination of four specimens, besides the holotype, that according to Weitzman and Palmer (1997) appear to be a rosy tetra, but the same authors emphasized that this needed confirmation.

The only paper available dealing with the phylogenetic relationships of the type species of *Ectreopopterus* is the molecular study of Thomaz *et al.* (2010) on the relationships of *Hollandichthys* Eigenmann 1909. *Hyphessobrycon uruguayensis* was included in their analysis due to the external similarity in the color pattern to *Hollandichthys*, forming longitudinal black stripes laterally on body in specimens larger than 35 mm SL. *Hyphessobrycon uruguayensis*, however, was not found closely related to *Hollandichthys*, but neither to *Hyphessobrycon eques* (Steindachner, 1882), a member of the rosy tetra clade (*sensu* Weitzman and Palmer 1997), making doubtful the decision to synonymize *Ectreopopterus* to *Hyphessobrycon*.

We herein revalidate the monotypic genus *Ectreopopterus*, and redescribe its type species *E. uruguayensis* based on the examination of the holotype and several series of additional specimens, including young and adult, from the lower río Uruguay and río Negro tributaries, as well as from small rivers draining to the río de La Plata, in Uruguay. An analysis of the phylogenetic relationships of the species is presented and a new generic diagnosis is proposed.

## Material and methods

Counts were taken as described by Fink and Weitzman (1974), with the exception of the number of scale rows below the lateral line, which were counted from the scale row ventral to lateral line to the scale row nearest the first pelvic-fin ray. Vertebral counts, supraneurals, gill rakers, teeth, and procurent caudal-fin ray counts were taken from cleared and stained specimens (c&s) prepared according to Taylor and van Dyke (1985). Vertebral counts include the four vertebrae integrated in the Weberian apparatus and the terminal centrum, which was counted as one vertebra. Scanning electronic micrographs (SEM) of teeth and jaws were taken from cleared and stained dissected specimens. X-rays of holotype were taken to count vertebrae.

Measurements were taken point-to-point with an electronic caliper to the nearest 0.01 mm on the left side of specimens when possible. Measurements are expressed as percents of standard length (SL) except for subunits of the head, which are recorded as percents of head length (HL). In the description, the asterisk indicates the value presented by the holotype. In the list of paratypes the number of whole specimens in the lot is followed by the number of examined specimens and c&s specimens. Institutional abbreviations are ANSP, Academy of Natural Sciences, Philadelphia, Philadelphia; BMNH, Natural History Museum [formerly British Museum (Natural History)], London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MTD-F, Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen [Staatliche Naturhistorische Sammlungen], Dresden; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; UFRGS, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., and ZVC, Departamento de Zoología de Vertebrados, Facultad de Humanidades y Ciencias, Universidad de Montevideo, Montevideo.

A phylogenetic analysis was performed adding the type species of *Ectreopopterus* and *Hyphessobrycon* to the character list and matrix of Mirande (2010). The analysis included equal weighting analysis and implied weighting, the last one following the same procedures described by Mirande (2009). Character states for *Ectreopopterus uruguayensis* and *Hyphessobrycon compressus* (Meek 1904) are given in Table 1. The numbers given for the characters follow Mirande (2010).

**TABLE 1.** Character states of *Ectreopopterus uruguayensis* and *Hyphessobrycon compressus*. Character list is the same of Mirande (2010). Multistate characters [01] are represented as “a”.

<i>Ectreopopterus uruguayensis</i>	00110010?1	0011000100	0001100001	0000100101	0000011100	0100000000	0201000011
?010000000	0010000110	10?1000010	0011000000	1000000100	0a?0011010	0001110100	001?000000
1010000000	00a0000201	0001000110	0101000001	00011a0000	0011000010	0100000101	0100010100
1000000000	0000000001	0101000100	1000000000	0000000001	0000000001	0000000001	0000000001
0101000100	0001110001	1000010001	0a00111a00	0000010101	0000101111	1100000011	2000000010
0001110000	000000a00?	0?00?0000?	?????				
<i>Hyphessobrycon compressus</i>	00110010?1	0011000100	0001100001	0000100100	0000011100	0100000000	00010a1011
?01000?00?	0010000110	10?1000010	0011000000	1000000100	0100011010	0001110100	001?000000
1010000000	0000000101	0001000110	0101000001	0001a00000	0011000010	0100000101	0100010110
100a000000	0000000001	0101000100	0001110001	100001000a	0a00111a00	0000010101	0000101100
0000000011	??0?100010	0001110000					

### *Ectreopopterus* Fowler 1943

*Ectreopopterus* Fowler 1943:313 (subgenus of *Megalampodus*; type species by original designation and monotypy: *Megalampodus uruguayensis*). Géry 1972:14 (redescription of the type species; new diagnosis for the subgenus). Géry 1977:586 (synonym of *Megalampodus*). Weitzman and Palmer 1997:234 (synonym of *Hyphessobrycon*).

**Diagnosis.** The following unambiguous apomorphies obtained through equal weighting analysis diagnose *Ectreopopterus* (ordered according to their consistency indexes). Characters 62, 67, 168, and 310 were also found as unambiguous autapomorphies of *Ectreopopterus* in the implied weighting analysis.

- (**Ch. 168:2; ci = 0.33**) Foramen in posterior region of metapterygoid that serves as passage for the *ramus mandibularis* of the *trigeminus* nerve forms an incomplete arch, bordered posteriorly by the hyomandibula (Fig. 2). This foramen is situated entirely within the metapterygoid among characid fishes lacking a supraorbital. The condition found in *Ectreopopterus* is apomorphic, and a reversal, since the foramen opening posteriorly is found in several basal lineages of the Characidae (e.g. *Brycon* Müller and Troschel 1844, *Bryconops* Kner 1858, and *Iguanodectes* Cope 1872; see Mirande 2010). This condition was found homoplastically in *Bryconamericus scleroparius* (Regan 1908) and in *Pseudocorynopoma doriae* Perugia 1891.

- (**Ch. 310:1; ci = 0.10**) Pectoral-fin rays bearing hooks. Although the presence of hooks in the fin rays is a condition shared by most characid fishes (Malabarba and Weitzman 2003), its presence in the pectoral fin rays is not usual and was found by parsimony as diagnostic for *Ectreopopterus*. It was found homoplastic in *Astyanax* cf. *asuncionensis* Géry 1972, *A. chico* Casciotta and Almirón 2004, *A. lineatus* (Perugia 1891), *A. troya* Azpelicueta, Casciotta and Almirón 2002, *Bario steindachneri* (Eigenmann 1893), *Bryconamericus iheringii* (Boulenger 1887), *B. rubropictus* (Berg 1901), *B. thomasi* Fowler 1940, *Hyphessobrycon luetkenii* (Boulenger 1887), *H. socolofi* Weitzman 1977, and *Nematocharax venustus* Weitzman, Menezes and Britski 1986 (Mirande 2010).

- (**Ch. 62:2; ci = 0.06**) Posterior margin of second infraorbital posteroventrally oblique and second infraorbital ventrally bordering anterior region of third infraorbital (Fig. 3). This condition is usually associated with a long maxilla, and is found homoplastic in *Exodon paradoxus* Müller and Troschel 1844, *Hollandichthys multifasciatus* (Eigenmann and Norris 1900), *Oligosarcus* spp., and several genera of the Characinae.

- (**Ch. 67:0; ci = 0.03**) Fourth infraorbital (Fig. 3) more developed longitudinally than dorsoventrally (*versus* longer dorsoventrally than longitudinally). Although apomorphic for *Ectreopopterus*, this character is broadly distributed among Characidae.

- (**Ch. 104:1; ci = 0.03**) Ascending process of premaxilla reaching just anterior end of nasal (*versus* reaching at least one-third of length of nasal). Although apomorphic for *Ectreopopterus*, this character is broadly distributed among Characidae.

- (**Ch. 91:1; ci = 0.02**) Lateral line interrupted (*versus* complete). Although highly variable in Characidae, this character was recovered as one of the autapomorphies for *Ectrepopterus*.

### ***Ectrepopterus uruguayensis* Fowler 1943**

(Figs. 1–6; Table 2)

*Megalamphodus uruguayensis* Fowler 1943:313 (type locality: Uruguay, no further locality data available; type species of the subgenus *Ectrepopterus* by original designation and monotypy; mistyped also as *Magalamphodus uruguayensis*).

*Megalamphodus (Ectrepopterus) uruguayensis*. Géry 1972:14 (redescription of holotype).

*Megalamphodus uruguayensis*. Géry 1977:586 (in key).

*Hyphessobrycon uruguayensis*. Weitzman and Palmer 1997:234 (listed as a valid species probably belonging to the rosy tetra group). Thomaz *et al.* 2010 (phylogeny based on DNA sequences).

**Diagnosis.** The same for the genus. The larger number of maxillary teeth (6–11) and the presence of longitudinal, wavy stripes laterally on body in larger specimens further distinguish this species from several characids.

**Description.** Morphometric data are summarized in Table 2. Body compressed and elongate; greatest body depth near to dorsal-fin origin. Dorsal head profile nearly straight. Dorsal body profile convex from supraoccipital bone to base of last dorsal-fin ray and straight from this point to adipose-fin origin. Ventral profile of head smoothly convex. Ventral body profile slightly convex to nearly straight from pectoral-fin origin to pelvic-fin origin, and straight to anal-fin origin. Body profile along anal-fin base posterodorsally slanted. Caudal peduncle elongate, nearly straight to slightly concave along dorsal and ventral margins.

**TABLE 2.** Morphometric data of holotype (H) and non-types specimens of *Ectrepopterus uruguayensis*. SD = Standard deviation. The range not includes the holotype.

Character	H	n	Range	Mean	SD
Standard length (mm)	29.2	86	23.4–47.4	32.1	–
Percents of Standard Length					
Predorsal distance	56.6	86	57.0–61.3	59.3	0.9
Prepelvic distance	50.7	86	49.1–55.9	52.4	1.2
Prepectoral distance	30.6	86	27.7–34.1	31.9	1.5
Preanal distance	65.7	86	62.7–72.7	67.7	1.4
Depth at dorsal-fin origin	41.4	86	37.5–48.5	42.4	2.3
Caudal peduncle depth	12.8	85	11.6–14.6	12.9	0.6
Caudal peduncle length	10.6	86	7.4–10.6	8.9	2.5
Anal-fin base	32.8	86	29.9–35.1	32.4	1.2
Dorsal-fin length	33.5	83	29.3–35.7	31.9	2.1
Pelvic-fin length	18.8	86	16.0–21.3	18.5	1.0
Pectoral-fin length	21.6	86	17.3–24.3	21.1	1.1
Head length	30.8	86	27.5–32.8	30.4	1.2
Percents of Head Length					
Snout Length	21.3	86	19.7–27.4	23.8	1.3
Upper jaw length	56.1	86	50.2–57.3	53.2	1.3
Orbital diameter	38.3	86	33.2–41.3	38.1	1.6
Interorbital width	30.4	86	28.1–34.9	31.7	1.6

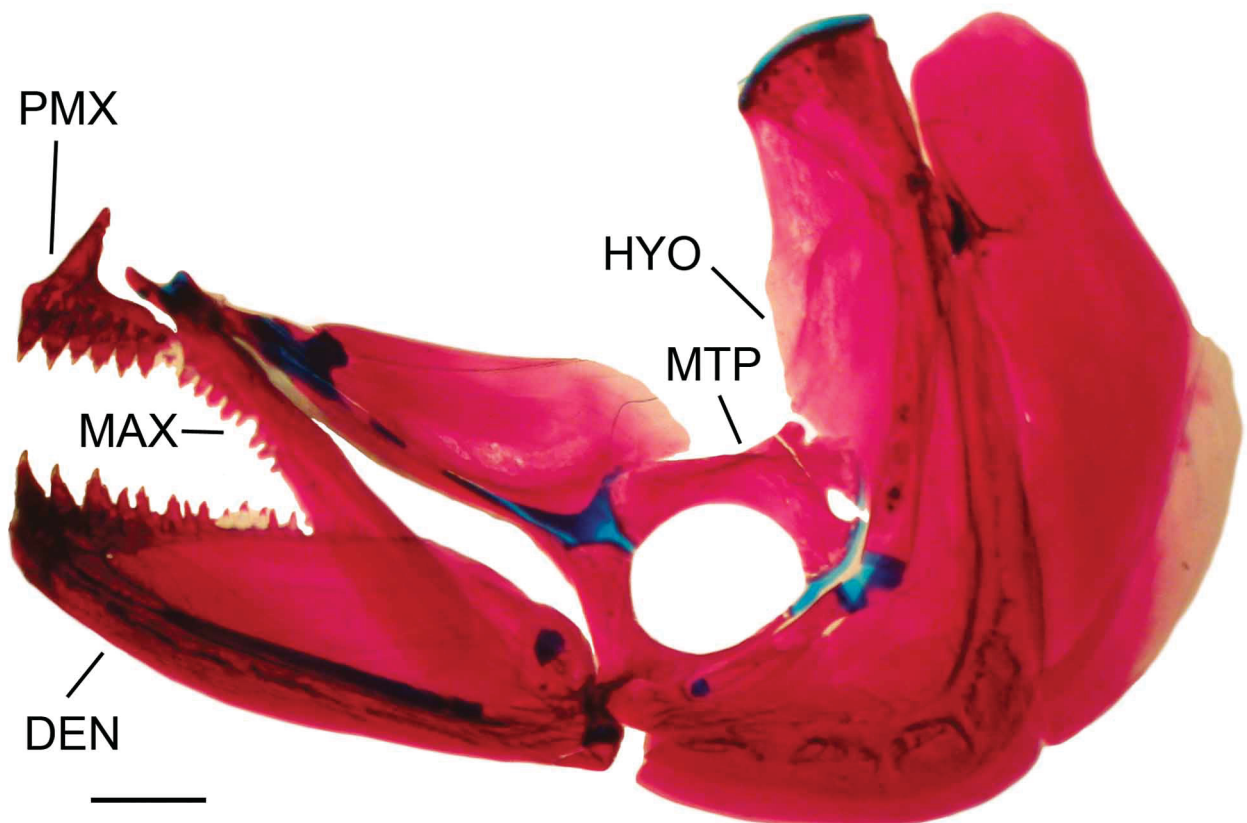
Mouth terminal, lower jaw projecting slightly more than upper jaw. Maxilla long and slightly curved aligned at angle of approximately 45 degrees relative to longitudinal body axis. Maxilla slightly widened anteroposteriorly, and extends to junction of infraorbital 2 and 3.



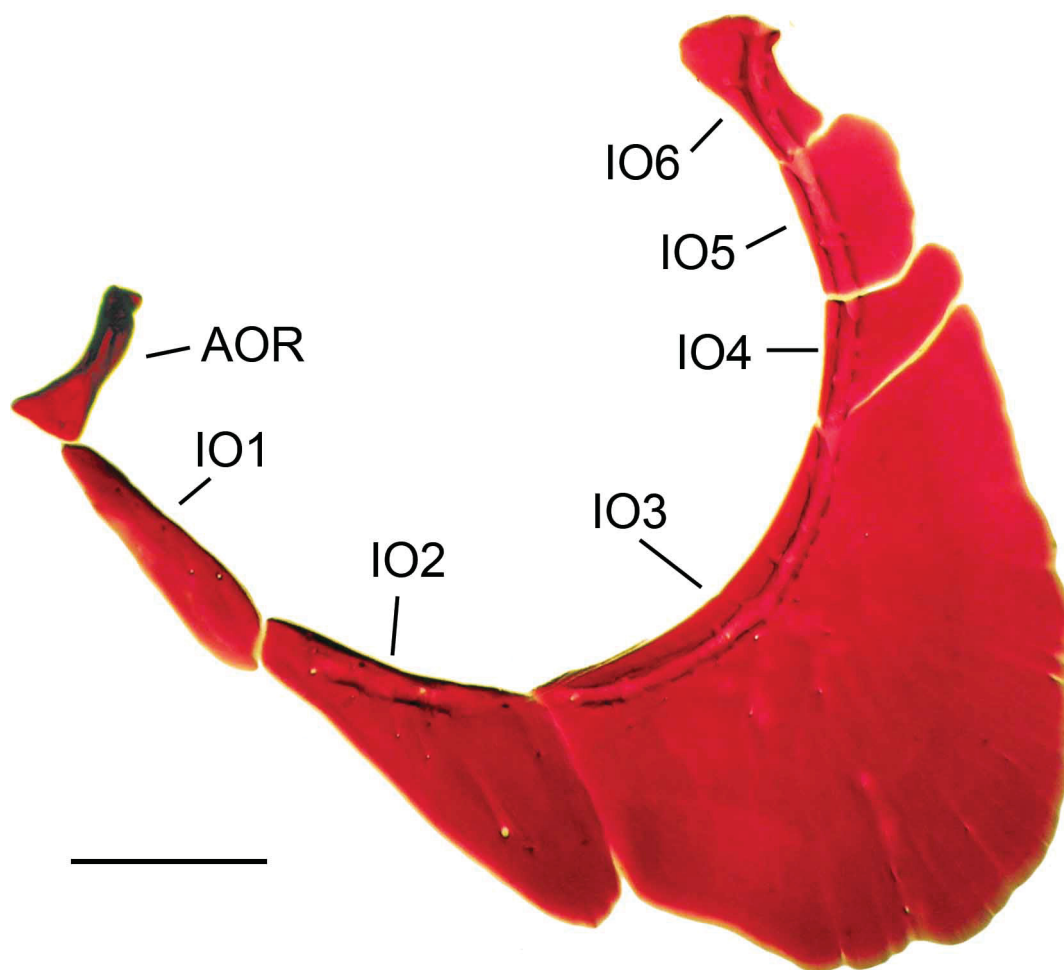
Premaxilla with one or two tooth rows: outer row, when present, with one to two tricuspid teeth; inner row with six to seven tricuspid teeth (7\*), gradually decreasing in length from first to fourth or fifth teeth and last two smaller. Maxilla with six to eleven (8\*, mode = 10) tricuspidate teeth; and last five or six uni- to tricuspid teeth. Four or five anteriormost dentary teeth larger, tricuspid, followed by one or two medium sized tricuspid teeth, and eight to 13 teeth with one to three cusps. Central cusp in all teeth two to three times longer and broader than other cusps. All cusp tips slightly curved posteriorly towards oral cavity (Fig. 4).



**FIGURE 1.** *Ectrepopterus uruguayensis*, ANSP 70331, holotype, female, 29.2 mm SL, Uruguay. Photo by K. Luckenbill.



**FIGURE 2.** *Ectrepopterus uruguayensis*, UFRGS 8578, 37.4 mm SL, male. Lower and upper jaws showing the premaxilla (PMX), maxilla (MAX) and dentary (DEN), and suspensorium showing the foramen in posterior region of metapterygoid (MTP) forming an incomplete arch and bordered posteriorly by the hyomandibula (HYO), left side. Scale bar = 1 mm.

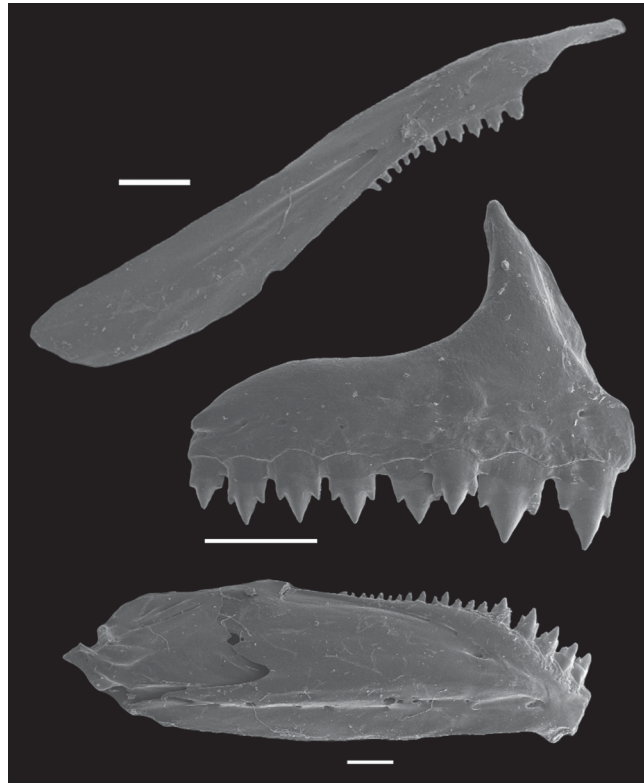


**FIGURE 3.** *Ectrepopterus uruguayensis*, UFRGS 8578, 37.4 mm SL, male. Infraorbital series (IO1–6) and antorbital (AOR), left side. Scale bar = 1 mm.

Dorsal-fin rays ii,8–10 (ii,9\*; n = 93; ii,8 and ii,10 in one specimen each); first unbranched ray approximately one-half length of second ray. Dorsal-fin origin located at middle of SL and posterior to vertical through pelvic-fin origin. Distal margin of dorsal fin slightly convex. Adipose-fin located approximately at vertical through insertion of last anal-fin ray. Pectoral-fin rays i,10–12\* (mode = 10, n = 93). Pelvic-fin rays i,6 or 7\* (mode = 7, n = 93). Pelvic-fin origin located anterior to vertical through dorsal-fin origin. Anal-fin rays iii–v,19–26 (22\*, rarely 19 or 24–26, mode = 22, n = 93). First unbranched ray normally only apparent in cleared and stained specimens. Anal-fin origin posterior to vertical through base of last two dorsal-fin ray. Caudal-fin forked, lobes similar in size, with 18–20 principal rays (19\*, two with 18 and one with 20, n = 92). Dorsal procurrent rays 9–11 (mode = 10, n = 10), and ventral procurrent rays 8–10 (mode = 9, n = 10).

Scales cycloid, moderately large. Lateral line incomplete, perforated scales 5–9 (8\*, one specimen with 5 and one specimen with 9, mode = 6, n = 93). Longitudinal scale series including pored scales 32\*–36 (mode = 33, n = 93). Scale rows between dorsal-fin origin and lateral line 6 or 7\* (mode = 6, n = 93); scale rows between lateral line and pelvic-fin origin 4–6 (5\*, mode = 5, n = 93). Predorsal scales 10\*–13, arranged in regular series (mode = 11, n = 82). Scale rows around caudal peduncle 14\* (n = 93). Scale sheath along anal-fin base 6–12 (8\*, mode = 8) scales in single series, extending to base of fifth to tenth branched rays.

Precaudal vertebrae 16\* or 17 (mode = 16, n = 11); caudal vertebrae 16 or 17\* (mode = 17, n = 11); total vertebrae 33\* or 34 (mode = 33, n = 11). Supraneurals 5 or 6 (mode = 6, n = 10). Gill rakers on upper limb of outer gill arch 5 or 6 (mode = 6), and on lower limb 9–11 (mode = 9, n = 10). Ventral extent of third infraorbital reaching horizontal arm of preopercle, but not reaching the laterosensory canal of preopercle. Fontanels forming slightly narrow groove; parietal little longer than frontal. Frontals not contacting anteriorly to frontal fontanel.



**FIGURE 4.** *Ectreopopterus uruguayensis*, MCP 31907, 38.5 mm SL, male. Scanning electronic micrograph of lower and upper jaws, right side. Scale bars = 0.5 mm.

**Color in alcohol.** The holotype is discolored, except for the humeral spot (Fig. 1). Color description based on non-type specimens (Fig. 5). Dorsal and dorsolateral portion of head and body pigmented dark brown. Scales on lateral and dorsal surface of body with scattered dark brown chromatophores. In some specimens larger than 35.0 mm SL the dorsal and ventral border of scales are dark brown pigmented forming a wavy, striped pattern between longitudinal rows of scales, more conspicuous in middle portion of body (Fig. 5). One narrow humeral spot vertically elongate, located over third to fourth lateral line scales and extending over two longitudinal series of scales above and below of lateral line. Midlateral body stripe very narrow extending from posterior middle region of body to base of median caudal-fin rays, wide and more densely pigmented on caudal peduncle forming a triangle spot. Anteriorly directed chevron-shaped marks along the midlateral body. Small black chromatophores scattered over rays of all fins. Caudal-fin rays darkened black in the distal portion. Adipose-fin smoothly dark black pigmented along the distal border.

**Color in life.** Color pattern similar to described for alcohol preserved specimens. Overall body and head color pattern silvery to golden (Figs. 5 and 6). Chromatophores distribution pattern of head, body and fins as described above for alcohol preserved specimens. Eye with upper third of iris iridescent red. Dorsal fin yellowish. Pectoral fin hyaline. Pelvic fin orangish. Anal fin yellowish, more intense along proximal half of most anterior anal-fin rays. Adipose fin yellowish. Caudal fin yellowish, mostly at the proximal half of the dorsal and ventral caudal-fin lobes; middle caudal-fin rays and distal third portion or distal half of caudal-fin rays with dark black melanophores (Figs. 5 and 6). Wavy, striped pigmentation pattern along the scales is not clearly discernible in living specimens.

**Sexual dimorphism.** Mature males of *Ectreopopterus uruguayensis* are recognized by the presence of small bony hooks on all rayed fins (absent in females). Mature males present bony hooks in the third distal portion of the first to fifth branched rays, and in the distal portion of all pectoral-fin rays. Pelvic fin usually bearing bony hooks along ventromedial border of the unbranched and first to fourth branched rays. Anal-fin rays bearing one small, elongate, retrorse bony hook along posterolateral border of each segment of lepidotrichia, usually along last unbranched ray to last branched ray, in the distal portion of all caudal-fin rays, and in the two posteriormost procurent caudal-fin-rays. Hooks usually located along of distal portion of each ray. Anal-fin profile nearly straight in males and smoothly concave in females. The presence of bony hooks is often found in males, but only



mature males (specimens larger than 33.0 mm SL) possess bony hooks on all rayed fins. Pectoral-fin tip reaching pelvic-fin origin in males but not in females. Pelvic-fin tip surpass anal-fin origin in males but not in females. Males and females also differ by anal-fin profile, which is nearly straight in males and smoothly concave in females. Gill glands were not found on first gill arch on both mature males and females.



**FIGURE 5.** *Ectreoptherus uruguayensis*, UFRGS 8073, 42.9 mm SL, arroyo de las Tunas on road 31, tributary of río Arapey Grande, Salto, Salto, Uruguay. The same specimen photographed alive (above) and six years after fixation in formalin and preservation in ethanol 70%.

**Distribution.** *Ectreoptherus uruguayensis* occurs in the lower tributaries of the río Uruguay (río Cuareim, río Salto, and río Negro basins), and río de La Plata (río Santa Lucía and arroyo Pand), in Uruguay (Fig. 7). The Uruguay River basin in Brazil has been extensively sampled for the last 20 years, with intensive collecting undertaken in some localities, and so far there are no records of the species in this country. Menni (2004) listed *Hyphessobrycon uruguayensis* (= *E. uruguayensis*) for Argentina without any specific location or list of examined material.

**Ecological notes.** *Ectreoptherus uruguayensis* inhabits streams, and occurs in semi-lentic and lotic shallow areas (up to 1.2 m deep) with moderate submerged vegetation and riparian vegetation composed by trees and

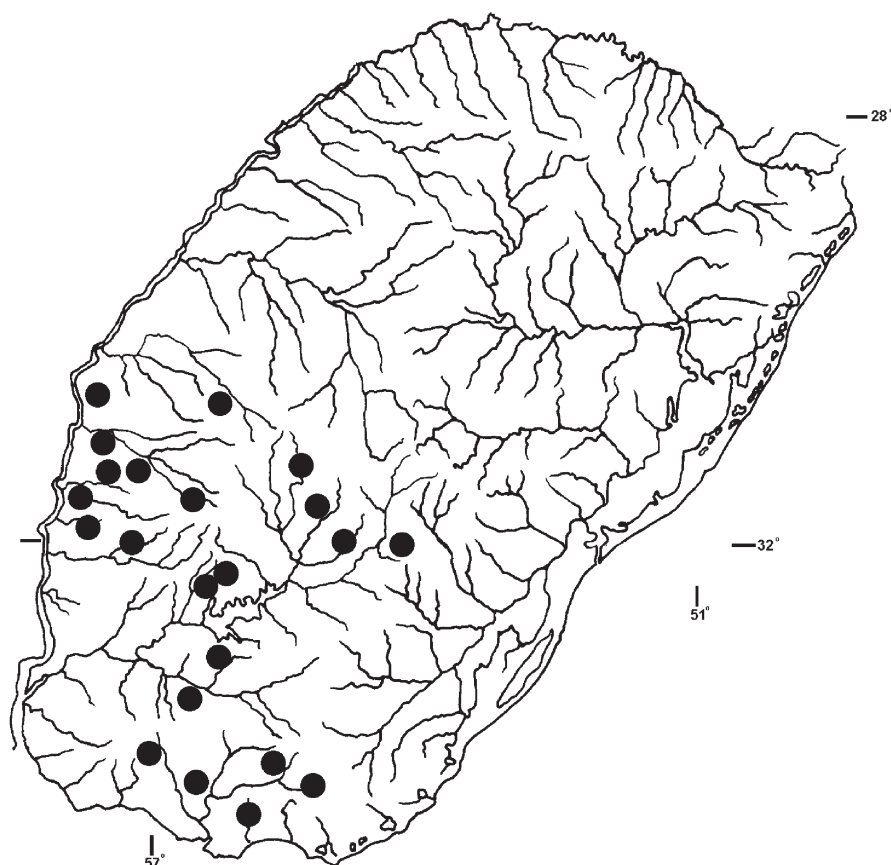


shrubs or absent. The streams have transparent water, and bottom with mud, some stretches with sand or gravel. Water temperature measured during field work ranged from 10 to 30°C, depending on the season. The pH was found around 7 in the neutral range. Keeping these conditions under consideration, *Ectrepopterus uruguayensis* can be easily kept in aquaria up to eight years. This species is usually collected in small numbers in natural habitats. Observations in aquaria (TOL) showed that, contrary to many other characids, it does not form schools, but rather specimens stay mainly alone, without showing territorial behavior.



FIGURE 6. *Ectrepopterus uruguayensis*, aquarium live specimen, not preserved.

**Material examined.** All from Uruguay: ANSP 70331, holotype, female, 29.2 mm SL, 1935, F. Felippone. MCP 13080, 5 (1 c&s), 27.7–36.5 mm SL, arroyo Catalán, puente de la ruta 30, Artigas, ca. 30°50'S 56°14'W, 9 Jul 1987, L. H. Amato. MCP 31907, 3 (1 c&s), 33.3–39.7 mm SL, arroyo Salsipuedes, tributary of the río Tacuarembó, Tacuarembó, 32°20'39"S 56°15'13"W, 15 Aug 2002, P. Laurino *et al.* MCP 31915, 35.9 mm SL, arroyo Catalán Grande, Artigas, 30°50'40"S 56°14'30"W, 16 Aug 2002, P. Laurino *et al.* MCP 33504, 2, 30.2–35.9 mm SL, arroyo Saucedo, Salto, 31°06'28"S 57°30'25"W, 17 Mar 2003, P. Laurino *et al.* MCP 33505, 6 (2 c&s), 23.6–29.1 mm SL arroyo Palomas (loc 2), Salto, 31°04'43"S 57°37'26"W, 17 Mar 2003, P. Laurino *et al.* MCP 33506, 4, 27.1–28.7 mm SL, arroyo Palomas (loc 1), Salto, ca. 31°03'16"S 57°37'43"W, 17 Mar 2003, P. Laurino *et al.* MCP 33507, 4, 25.5–33.3 mm SL, arroyo Cardoso, San José, 34°24'50"S 56°26'49"W, 23 Mar 2003, E. Lartigau *et al.* MCP 36790, 33.8 mm SL, arroyo Pando, Canelones, 34°44'19"S 54°56'27"W, 26 Aug 2004, P. Laurino *et al.* MCP 36791, 2, 38.7–42.1 mm SL, creek near Paso de San Borja, Durazno, 33°24'57"S 56°25'57"W, 22 Aug 2004, P. Laurino *et al.* MCP 36792, 35.6 mm SL, arroyo Pando, Canelones, 34°42'12"S 55°56'43"W, 31 Aug 2004, T. O. Litz *et al.* MCP 36795, 13, 29.2–43.4 mm SL, ditch between arroyo Salsipuedes and ruta 5 Km 289.5, tributary of the río Tacuarembó, Tacuarembó, 32°29'13"S 56°22'44"W, 22 Aug 2004, P. Laurino *et al.* MCP 36796, 8, 28.8–35.8 mm SL, arroyo Catalán Grande, Artigas, 30°50'40"S 56°14'30"W, 23 Aug 2004, P. Laurino *et al.*; MTD-F 27461–27466, 6, 25.9–35.6 mm SL, arroyo Palomas (loc 2), Salto, 31°04'43"S 57°37'26"W, 17 Mar 2003, P. Laurino *et al.* UFRGS 7169, 4, 29.0–32.0 mm SL, arroyo Mestre de Campo, on road to Polanco of YI, drainage of río YI, Durazno, 33°24'55"S 56°12'06"W, 29 May 2005, L. R. Malabarba *et al.* UFRGS 7170, 11, 30.2–40.0 mm SL, arroyo affluent to arroyo Mestre de Campo, on road to Polanco of YI, drainage of río YI, Durazno, 33°23'S 56°13'W, 29 May 2005, L. R. Malabarba *et al.* UFRGS 7171, 23, 36.2–44.5 mm SL, arroyo on road 26 ca. 59 km of Melo, between arroyos Saule and Fratile Muerto, Melo, 32°17'39"S 54°44'59"W, 28 May 2005, L. R. Malabarba *et al.* UFRGS 7172, 2, 36.4–39.6 mm SL, marginal pool and arroyo Corrales, on road 27, drainage of río Tacuarembó, Rivera, 31°23'26"S 55°15'14"W, 27 May 2005, L. R. Malabarba *et al.* UFRGS 7343, 1, 36.7 mm SL, río Caraguatá,



**FIGURE 7.** Drainages of laguna dos Patos system (right upper) in Rio Grande do Sul State, Brazil and left part of rio Uruguay basin in Uruguay and Brazil, showing the distribution of *Ectrepopterus uruguayensis*. Some symbols represents more than one lot and locality.

rio Tacuarembó basin, Tacuarembó, 32°09'29"S 55°01'27"W, 28 May 2005, L. R. Malabarba *et al.* UFRGS 7474, 30.6 mm SL, arroyo Cuñapiru, rio Tacuarembó basin, km 12.3 road 27, Rivera, Rivera, 31°02'21"S 55°29'31"W, 27 May 2005, L. R. Malabarba *et al.* UFRGS 7506, 47.9 mm SL; UFRGS 10564, 2 ethyl alcohol anhydrous, 38.2–40.0 mm SL, arroyo on road 26 about 59 km of Melo, Cerro Largo, 32°17'39"S 54°44'59"W, 28 May 2005, L. R. Malabarba *et al.* UFRGS 7767, 3, 37.2–40.5 mm SL, arroyo Cuaró Grande on road 4, tributary of rio Quaraí, Artigas, Artigas, 30°47'03"S 56°46'54"W, 8 Sep 2005, L. R. Malabarba *et al.* UFRGS 7785, 1, 37.1 mm SL; UFRGS 12345, 1 ethyl alcohol anhydrous, 38.2 mm SL, arroyo Carpinchuri, tributary of rio Uruguay on road 3, Paysandu, Paysandu, 31°40'38"S 57°53'30"W, 20 Sep 2005, L. R. Malabarba *et al.* UFRGS 7899, 1, 39.7 mm SL, arroyo Chapicuy Chico, tributary of rio Uruguay on road 3, Paysandu, Paysandu, 31°37'20"S 57°52'51"W, 10 Sep 2005, L. R. Malabarba *et al.* UFRGS 7909, 9, 33.1–40.2 mm SL, cañada Cecilia on road 3, km 512, Salto, Salto, 31°16'01"S 57°46'42"W, 9 Sep 2005, L. R. Malabarba *et al.* UFRGS 7918, 2, 38.9–44.4 mm SL, cañada on road 4, tributary of rio Queguay Grande, Paysandu, Paysandu, 32°12'25"S 57°12'47"W, 10 Sep 2005, L. R. Malabarba *et al.* UFRGS 7945, 36.9 mm SL, cañada on road 4, tributary of rio Queguay Chico, Paysandu, Paysandu, 32°01'57"S 57°19'30"W, 10 Sep 2005, L. R. Malabarba *et al.* UFRGS 7985, 53, 29.8–44.3 mm SL, arroyo Guaviyú on road 3, tributary of rio Uruguay, Artigas, Artigas, 30°37'51"S 57°41'18"W, 9 Sep 2005, L. R. Malabarba *et al.* UFRGS 8009, 40.2 mm SL, arroyo los Chanchos on road 3, rio Daymán basin, Paysandu, Paysandu, 31°28'34"S 57°54'06"W, 10 Sep 2005, L. R. Malabarba *et al.* UFRGS 8073, 9, 33.5–42.9 mm SL, arroyo de las Tunas on road 31, tributary of rio Arapey Grande, Salto, Salto, 31°20'04"S 57°19'36"W, 8 Sep 2005, L. R. Malabarba *et al.* UFRGS 8105, 2, 42.3–46.4 mm SL, arroyo on road 4, tributary of rio Valentin Grande, Salto, Salto, 31°16'32"S 57°09'22"W, 8 Sep 2005, L. R. Malabarba *et al.* UFRGS 8578, 27 (4 c&s), 39.3–40.8 mm SL, arroyo Tala on road 31 between Salto city and Artigas, 31°23'09"S 57°33'46"W, L. R. Malabarba *et al.* UFRGS 10973, ethyl alcohol anhydrous, 32.8 mm SL, arroyo Tala on road 31, tributary of rio Uruguay, Salto, Salto, 31°23'09"S 57°33'46"W, 8

Sep 2005, L. R. Malabarba *et al.* UFRGS 11129, 2 ethyl alcohol anhydrous, 33.3–38.9 mm SL, arroyo Corrales and lateral puddles on road 27, río Tacuarembó basin, Rivera, Rivera, 31°23'26''S 55°15'14''W, 27 May 2005, L. R. Malabarba *et al.* ZVC-P 423, 8, 28.8–38.8 mm SL, arroyo Bolón, tributary of the arroyo Tomás Cuadra, río Negro drainage, ca. 33°12'S 56°10'W, E. Messner. ZVC-P 1464, 16 (2 c&s), 31.3–47.4 mm SL, arroyo Higuera, tributary of the arroyo Carpintería, río Negro drainage, Tacuarembó, ca. 31°45'S 55°13'W, 5 Oct 1959, E. Messner. ZVC-P 1769, 31.8 mm SL, río Santa Lucía, Arequita, Levalleja, ca. 34°20'S 55°15'W, Carbonell. ZVC-P 2975, 4, 25.6–27.5 mm SL, Estancia San Francisco, 5 km W from Casupá, Florida, ca. 34°05'S 55°40'W, 12 Apr 1981, E. Lessa & D. Lisandro. ZVC-P 5267, 53, 16.1–24.3 mm SL, arroyo Mahoma Chico, tributary of the río San José, San José, ca. 34°02'S 56°58'W, 4 Jan 1953.

## Discussion

The establishment of relationships among characid fishes is a complex task due to the species richness, conservative morphology, and long period of evolution of the group. These facts combined apparently favored the occurrence of repeated and independent events of morphological changes along different lineages in the family (Weiss *et al.* in press), that resulted in extremely elevated levels of morphological homoplasies (*e.g.* Miranda 2010).

This state of uncertainty, however, is not the same among all characid members. There is a well corroborated large monophyletic unit among characids that include all species lacking a supraorbital (Malabarba and Weitzman 2003, Javonillo *et al.* 2010, Miranda 2010), embracing most small sized species (Azevedo 2011). Among these, monophyly of some clades has been supported through phylogenetic studies using different sources of information. Monophyly of the Clade A of Malabarba and Weitzman (2003), named Stevardiinae by Miranda (2009, 2010) has been supported by the morphological data in those studies, as well as by molecular (Javonillo *et al.* 2010; Thomaz *et al.* 2010) and sperm morphology analyses (Baicere-Silva *et al.* 2011). The recognition of the subfamilies Aphyocharacinae, Characinae, and Cheirodontinae also seems to be congruent at some level within different studies (Malabarba 1998; Calcagnotto *et al.* 2005; Javonillo *et al.* 2010, Miranda 2010), even though with disputing hypotheses regarding internal relationships or in their compositions. A few small characid subfamilies proposed or redefined by Miranda (2010) still needs further tests of monophyly (Aphyoditeinae, Gymnocharacinae, Heterocharacinae, and Rhoadsiinae) based on new or complementary data.

The main unsettled portion in characid phylogeny remains on some of the genera placed in Tetragonopterinae by Eigenmann (1921) and Géry (1977), including four of the most species rich genera of the Characidae: *Astyanax* Baird and Girard 1854, *Hemigrammus* Gill 1858, *Hyphessobrycon*, and *Moenkhausia* Eigenmann 1903. This unsettled portion of the Characidae forms the clade C of Javonillo *et al.* (2010) and is spread over successive branches in the middle portion of the cladogram in the phylogeny of Miranda (2010) named respectively as the *Bramocharax* clade, *Pseudochalceus* clade, Rhoadsiinae, Tetragonopterinae, *Hyphessobrycon luetkenii* clade, *Astyanax paris* clade, *Astyanax* clade, *Bryconamericus scleroparius* clade, and Gymnocharacinae.

*Ectreopopterus uruguayensis* shares the synapomorphic lack of a supraorbital (Malabarba and Weitzman 2003). However, a molecular analysis using the genes *Sia*, *Trop*, and 16S (Thomaz *et al.* 2010) proved it to be part of the large unresolved portion of the Characidae, corresponding to clade C of Javonillo *et al.* (2010). Such a status for *Ectreopopterus* seems to be further supported by the lack of the morphological synapomorphies of the Aphyocharacinae, Characinae, Cheirodontinae, or Stevardiinae, or those of the Aphyoditeinae, Gymnocharacinae, Heterocharacinae, and Rhoadsiinae as defined by Miranda (2010).

*Ectreopopterus uruguayensis* has been so far hypothesized as belonging to *Hyphessobrycon* or to its current junior synonym *Megalamphodus* (Weitzman and Palmer 1997). *Hyphessobrycon* includes almost 130 valid species (Eschmeyer and Fricke 2011), but has been repeatedly recovered as polyphyletic in recent phylogenies (*e.g.* Javonillo *et al.* 2010, Miranda 2010). The genus is currently defined by a combination of non-exclusive characters proposed by Eigenmann (1918), as premaxillary teeth in two rows, the inner series with five teeth; second suborbital (= third infraorbital *sensu* Weitzman 1962) not in contact with the preopercle below; few maxillary teeth; lateral line incomplete; caudal fin not covered with scales; and adipose fin present. *Ectreopopterus uruguayensis* does not fit in this traditional diagnosis of *Hyphessobrycon* in possessing a long toothed maxilla (6–11 teeth), instead of few maxillary teeth (Figs. 2 and 4).



The inclusion of the type species of *Ectrepopterus* in the “rosy tetra clade by Weitzman and Palmer (1997) and consequently turning *Ectrepopterus* a synonym of *Hyphessobrycon* is also unsupported. The exam of freshly collected series of specimens (Figs. 5 and 6) including adults and juveniles, showed that *Ectrepopterus uruguayensis* lacks the rosy tetra color pattern (red or reddish brown), the long and high dorsal fin with a black spot, and the elongate anterior anal-fin lobes used by Weitzman and Palmer (1997) in defining the “rosy tetra clade”.

Possible synonym of *Ectrepopterus* to *Hyphessobrycon* was further tested herein with the inclusion of *Ectrepopterus uruguayensis* and of the type species of *Hyphessobrycon*, *H. compressus*, in the 360 morphological characters matrix of Miranda (2010), along with other 160 species. The equal weighting parsimony analysis recovered *Ectrepopterus uruguayensis* forming a clade along with *Nematobrycon* Eigenmann 1911 (one of the genera of the subfamily Gymnocharacinae proposed by Miranda 2010) and *Probolodus* Eigenmann 1911 in a large polytomy, and excluding *H. compressus*. Unambiguous characters found in defining *Ectrepopterus* in equal weighting analysis were 62(2), 67(0), 91(1), 104(1), 168(2), and 310(1), and are presented in the reformulated diagnosis of the genus.

The result of implied weighting analysis recovered *Ectrepopterus uruguayensis* forming a clade along with *Probolodus* and the Gymnocharacinae of Miranda 2010 (*Nematobrycon*, *Gymnocharacinus* Steindachner 1903, *Grundulus* Valenciennes 1846, and *Coptobrycon* Géry 1966). *Hyphessobrycon compressus* forms a clade along with the rosy tetras *H. eques* (Steindachner 1882), *H. socolofi*, and *H. pulchripinnis* Ahl 1937, and with *Hemigrammus unilineatus* (Gill 1858), thus refuting the synonym of *Ectrepopterus* and *Hyphessobrycon*. The inclusion of *Ectrepopterus* and *Probolodus* in a single clade along with the Gymnocharacinae, however, is weakly supported by two synapomorphies only, whose status is marked as unknown in the *Nematobrycon*, *Gymnocharacinus*, *Grundulus*, and *Coptobrycon*: the presence of bony hooks in the dorsal fin (Ch. 311:1) and caudal fin (Ch. 312:1) of adult males. Mature males of *E. uruguayensis* possess bony hooks in all rayed fins. The presence of hooks on the anal- and pelvic-fin rays is found in most genera and subfamilies of Characidae (Azpelicueta and Garcia 2000, Malabarba and Weitzman 2003, Miranda 2010), and usually represent a secondary sexual characters of males. Presence of small bony hooks in the dorsal- and caudal fin rays is known in a smaller number of taxa.

Additional characters useful in the recognition of *Ectrepopterus uruguayensis* include the possession of black wavy longitudinal stripes (or striped pattern, although some specimens can present only small black spots on lateral surface of body) between longitudinal rows of scales. Black longitudinal stripes are also found in *Astyanax lineatus* (Perugia, 1891), *A. kullanderi* Costa 1995, *A. superbus* Myers 1942, *Barrio steindachneri*, *Hyphessobrycon hexastichos* Bertaco and Carvalho 2005, *Hollandichthys multifasciatus*, *Markiana nigripinnis* (Perugia, 1891), *Moenkhausia agnesae* Géry 1965, *M. latissima* (Eigenmann 1908), *M. rara* (= *Tetragonopterus rarus*) Zarske, Géry and Isbrücker 2004, *M. simulata* (Eigenmann 1924), *Pseudochalceus lineatus* Kner 1863, and *Tetragonopterus lemniscatus* (= *T. rarus*) Benine, Pelicão and Vari 2004.

The lower lobe of the caudal fin larger than the upper lobe mentioned by Fowler (1943) for the diagnosis of *Ectrepopterus* is broadly found in the small Characidae (cf. Lima and Moreira 2003, fig. 9, for *Hyphessobrycon weitzmanorum*; Zanata and Ohara 2009, fig. 1, for *Jupiaba citrina*; Britski and Lima 2009, fig. 1, for *Hemigrammus silimoni*; Bertaco and Garutti 2007, fig. 1, for *Astyanax utiariti*). We found usually both lobes of equal size, but also some intrapopulation variation of this character, with some specimens showing lower lobe larger than upper lobe or vice-versa.

The proposal of revalidation of *Ectrepopterus* and removal from the synonym of *Hyphessobrycon* starts a deconstruction of the last polyphyletic genus into smaller and monophyletic units, and towards the recognition of a monophyletic *Hyphessobrycon* (by FRC and LRM). Although *Ectrepopterus* is being revalidated herein as a monotypic genus, its exclusion from the synonym of *Hyphessobrycon* is obligatory, since *Ectrepopterus uruguayensis* was not recovered as closely related to any other characid species currently assigned to *Hyphessobrycon*.

**Comparative material.** *Hemigrammus compressus*, FMNH 4641, holotype, 31.2 mm SL; FMNH 4642, 17 paratypes, 26.6–35.7 mm SL. *Hyphessobrycon bentosi*, USNM 120270, 3 syntypes, 22.3–24.4 mm SL. *Hyphessobrycon bifasciatus*, FMNH 54404, holotype, 33.5 mm SL. *Hyphessobrycon compressus*, UFRGS 9683, 4 c&s, 30.9–34.4 mm SL. *Hyphessobrycon compressus milleri*, CAS 70115, holotype, 31.3 mm SL. *Hyphessobrycon copelandi*, USNM 120271, 6 syntypes, 14.7–28.4 mm SL. *Hyphessobrycon ecuadoriensis*, CAS 61602, holotype,



23.2 mm SL; CAS 122776, 16 paratypes, 16.5–22.1 mm SL. *Hyphessobrycon elachys*, USNM 232393, holotype, 15.8 mm SL. *Hyphessobrycon eos*, FMNH 52795, holotype, 28.1 mm SL. *Hyphessobrycon erythrostigma*, ANSP 70208, holotype, 48.0 mm SL. *Hyphessobrycon georgettae*, ANSP 112186, 2 paratypes, 13.9–16.5 mm SL. *Hyphessobrycon hasemani*, ANSP 39230, holotype, 20.4 mm SL. *Hyphessobrycon panamensis*, USNM 120416, 2 paratypes, 25.4–25.7 mm SL. *Hyphessobrycon pyrrhonotus*, USNM 326184, 8 paratypes, 36.6–45.0 mm SL. *Hyphessobrycon rosaceus*, FMNH 52791, holotype, 28.6 mm SL; USNM 66194, paratype, 16.2 mm SL. *Hyphessobrycon serpae*, USNM 120269, 6 syntypes, 20.1–23.1 mm SL. *Hyphessobrycon socolofi*, USNM 216612, 5 paratypes, 30.5–39.2 mm SL. *Hyphessobrycon stegemanni*, USNM 195942, holotype, 31.1 mm SL. *Hyphessobrycon takasei*, USNM 198138, holotype, 30.0 mm SL. *Megalamphodus megalopterus*, FMNH 57823, holotype, 26.9 mm SL; FMNH 57824, 2 paratypes, 18.2–28.3 mm SL. *Megalamphodus micropterus*, CAS 98918, 6 paratypes, 21.3–23.7 mm SL. *Megalamphodus roseus*, ANSP 112496, 2 paratypes, 13.7–14.5 mm SL; ANSP 139704, paratype, 15.2 mm SL. *Megalamphodus sweglesi*, USNM 196090, holotype, 29.9 mm SL. *Tetragonopterus callistus*, BMNH 1900.4.14.63–68, 6 syntypes, 17.3–27.0 mm SL.

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## Literature cited

- Azevedo, M.A. (2011) Reproductive characteristics of characid fish species (Teleostei, Characiformes) and their relationship with body size and phylogeny. *Iheringia, Série Zoologia*, 100, 469–482.
- Azpelicueta, M.M. & Garcia, J.O. (2000) A new species of *Astyanax* (Characiformes, Characidae) from Uruguay river basin in Argentina, with remarks on hook presence in Characidae. *Revue suisse de Zoologie*, 107, 245–257.
- Baicere-Silva, C.M., Ferreira, K.M., Malabarba, L.R., Benine, R.C. & Quagio-Grassiotto, I. (2011) Spermatic characteristics and sperm evolution on the subfamily Stevardiinae (Ostariophysi: Characiformes: Characidae). *Neotropical Ichthyology*, 9, 377–392.
- Bertaco, V.A. & Carvalho, T.P. (2005) A new characid fish, *Hyphessobrycon hexastichos* (Characiformes: Characidae) from Chapada dos Parecis, Mato Grosso, Brazil. *Neotropical Ichthyology*, 3, 439–443.
- Bertaco, V.A. & Garutti, V. (2007) New *Astyanax* from the upper rio Tapajós drainage, central Brazil (Characiformes: Characidae). *Neotropical Ichthyology*, 5, 25–30.
- Britski, H.A. & Lima, F.C.T. (2008) A new species of *Hemigrammus* from the upper Rio Tapajós basin in Brazil (Teleostei: Characiformes: Characidae). *Copeia*, 2008, 565–559.
- Calcagnotto, D., Schaeffer, S.A. & DeSalle, R. (2005) Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. *Molecular Phylogenetics and Evolution*, 36, 135–153.
- Eigenmann, C.H. (1918) The American Characidae [Part 2]. *Memoirs of the Museum of Comparative Zoology*, 43, 103–208.
- Eigenmann, C.H. (1921) The American Characidae [Part 3]. *Memoirs of the Museum of Comparative Zoology*, 43, 209–310.
- Eschmeyer, W.N. & Fricke, R. (Eds.) (2011) *Catalog of Fishes. Electronic version – 10 February 2011*. California Academy of Sciences. Available from: <http://research.calacademy.org/ichthyology/catalog/fishcatmain.asp> (February 21, 2011)
- Fink, W.L. & Weitzman, S.H. (1974) The so-called Cheirodontin fishes of Central America with descriptions of two new species (Pisces: Characidae). *Smithsonian Contributions of Zoology*, 172, 1–46.
- Fowler, H.W. (1943) Notes and descriptions of new or little known fishes from Uruguay. *Proceedings of the Academy of Natural Science of Philadelphia*, 95, 311–334.
- Géry, J. (1972) Corrected and supplemented descriptions of certain characoid fishes described by Henry W. Fowler, with revisions of several of their genera. *Studies on the Neotropical Fauna*, 7, 1–35.
- Géry, J. (1977) *Characoids of the World*. T.H.F. Publications, Neptune City, NJ, 672p.

- Javonillo, R., Malabarba, L.R., Weitzman, S.H. & Burns, J.R. (2010) Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes), based on molecular sequence data. *Molecular Phylogenetics and Evolution*, 54, 498–511.
- Lima, F.C.T. & Moreira, C.R. (2003) Three new species of *Hyphessobrycon* (Characiformes: Characidae) from the upper rio Araguaia basin in Brazil. *Neotropical Ichthyology*, 1, 21–33.
- Malabarba, L.R. (1998) *Monophyly of the Cheirodontinae, characters and major Clades (Ostariophysi: Characidae)*. Pp. 199–233. In: Malabarba, L.R., Reis, R.E. Vari, R.P., Lucena, Z.M.S. & Lucena, C.A.S. (Orgs.). *Phylogeny and classification of Neotropical fishes*. Edipucrs, Porto Alegre, 603p.
- Malabarba, L.R. & Weitzman, S.H. (2003) Description of new genus with six new species from southern Brazil, Uruguay and Argentina, with a discussion of a putative characid clade (Teleostei: Characiformes: Characidae). *Comunicações do Museu de Ciências e Tecnologia da PUCRS, Série Zoologia*, 16, 67–151.
- Menni, R.C. (2004) *Peces y ambientes en la Argentina continental*. Monografías del Museo Argentino de Ciencias Naturales, No 5, Buenos Aires, 316p.
- Mirande, J.M. (2009) Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics*, 2, 574–613.
- Mirande, J.M. (2010) Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. *Neotropical Ichthyology*, 8, 385–568.
- Taylor, W.R. & van Dyke, G.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.
- Thomaz, A.T., Malabarba, L.R. & Bonatto, S.L. (2010) The phylogenetic placement of *Hollandichthys* Eigenmann 1909 (Teleostei: Characidae) and related genera. *Molecular Phylogenetics and Evolution*, 57, 1347–1352.
- Weiss, F.E., Malabarba, L.R. & Malabarba, M.C. (In press) Phylogenetic relationships of *Paleotetra*, a new characiform genus (Ostariophysi) with two new species from the Eocene-Oligocene of southeastern Brazil. *Journal of Systematic Palaeontology*.
- Weitzman, S.H. (1962) The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyology Bulletin*, 8, 1–77.
- Weitzman, S.H. & Palmer, L. (1997) A new species *Hyphessobrycon* (Teleostei: Characidae) from the Neblina region of Venezuela and Brazil, with comments on the putative ‘rosy tetra clade’. *Ichthyological Exploration of Freshwaters*, 7, 209–242.
- Zanata, A.M. & Ohara, W.M. (2009) *Jupiaba citrina*, a new species from rio Aripuanã, rio Madeira basin, Amazonas and Mato Grosso states, Brazil (Characiformes: Characidae). *Neotropical Ichthyology*, 7, 513–518.